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THE EVOLUTION OF ARTHROPODS AND THEIR RELATIVES WITH ESPECIAL REFERENCE TO INSECTS [1]

G. C. CRAMPTON, Ph.D.

Massachusetts Agricultural College

The two lines of descent which have culminated in the production of some of the most active and "dynamic" of living creatures, and those in which the psychic faculties have attained their highest degree of perfection, are represented by the vertebrate group Mammalia, at whose apex is man, and the invertebrate group Arthropoda, at whose apex are the Insecta. Since these are the great rival groups, contending for the possession of the earth, the tracing of the paths by which they have arrived at their present dominating positions affords one of the most fascinating chapters of the study of organic evolution. Concerning the ancestry of man, there is some degree of agreement of opinion in modern works upon the subject; but the recent investigations of Handlirsch, 1904–1908, are not in accord with those of his predecessors in the study of insect phylogeny, and since his views have received a surprisingly widespread acceptance, his work has served to revive the discussion of the ultimate derivation of the insectan type of animals.

There can be but little doubt that the insects and their arthropodan relatives are the descendants of ancestors related to the worm-like forms. These in turn were derived from lower worm-like ancestors resembling the members of the Rotifera-Platyhelminthes group. In the present state of our knowledge of the subject, it is hardly possible to state with any degree of certainty whether the ancestors of the worm-like forms were ultimately

[1] Contribution from the Entomological Laboratory of the Massachusetts Agricultural College, Amherst, Mass.

derived from the Cœlenterata-Porifera group—*i. e.*, from a cœlenterate (cnidarian ?) type of animal through *Ctenophora*-like (?) forms; or more directly from a colonial protozoan type through forms comparable to the "Mesozoa" and their relatives, such as *Dicyema*, etc.; although there is a strong probability that the lower worm-like forms arose from ancestors occupying a position intermediate between these types of animals. From the standpoint of evolution, the Rotifera and Platyhelminthes (also such worms as *Dinophilus*, etc.) are among the most important of the lower worm-like forms, since they have departed as little as any from the condition characteristic of the ancestors of the "Annelida" and many other invertebrates; and even the line of descent of the vertebrates themselves may ultimately lead back to forms not unlike the members of this group. A higher stage of development is represented by the "Annelida" (including the Sternaspididæ, *Gephyrea*, etc.), which are a group of the greatest phylogenetic importance due to the fact that their line of development is approached by, or is paralleled by, those of many other invertebrate groups, and to the fact that they have retained a great number of characteristics apparently typical of the ancestors of the Arthropoda. Their forebears probably occupied a position intermediate between the Rotifera and the Platyhelminthes, and indeed, some investigators have even placed the "archiannelid" *Dinophilus* among the planarian Platyhelminthes, although its closest affinities seem to be with the annelidan worms *Protodrilus* and *Polygordius*.

From their annelid-like forebears, there have branched off two important lines of descent, which have approached very close to the arthropodan type, and which have even been classed among the Arthropoda by some investigators. One of these lines of development is represented by the Onychophora, which are suggestively arthropod-like in many particulars, although they have retained many annelidan characters; while the other line

is represented by the Myzostomida, which are regarded by some authorities as occupying a position intermediate between the chætopod Annelida and the Tardigrada.

The position of the Tardigrada is still a subject of considerable discussion, and the decision of the matter depends largely upon the settling of the question whether the apparent simplicity of their organization is due to the retention of a primitively simple condition, or to a secondarily acquired simplicity brought about by reduction or degeneracy, etc. If the simplicity of the Tardigrada is a primitive one, there is much to be said in favor of placing them next to the Myzostomida in the Myzostomida-Onychophora group; but whether the Linguatulida should also be included in this group seems very doubtful.

From the resemblance of the adults to Eriophyid mites, and of the immature forms to such short-bodied mites as *Phytoptus*, etc., many recent authorities would place the Linguatulida near the Acarina—a highly modified group far removed from the base of the arthropodan stem. If this view is correct, the apparent simplicity of the Linguatulida is to be regarded as the result of a reduction or degeneration rather than the retention of a primitive condition, in forms so far removed from the base of the arthropodan stem; and if the simplicity of the Tardigrada is primitive, while that of the Linguatulida has been secondarily acquired through reduction or degeneracy, the apparent resemblance between the Tardigrada and Linguatulida must be regarded as the result of convergence, or parallelism, rather than of consanguinity. Under these conditions the Linguatulida could not be grouped with the Tardigrada, if the latter are placed next to the Myzostomida in the Myzostomida-Onychophora group; but if the apparent simplicity of the Tardigrada is also due to reduction or degeneracy, they too might be placed with the Linguatulida near the mites—although this does not appear to be very probable from our present knowledge of the subject. It is quite ap-

parent, however, that the matter needs considerable further investigation before this question can be definitely determined.

The affinities of the molluscan group are somewhat obscure, but the study of their immature stages would indicate that the Mollusca are rather distantly related to the Chætopoda, *Gephyrea*, "Polyzoa," and other annelid-like forms. If this be true, their line of development apparently likewise extends back to forebears similar to the members of the Rotifera-Platyhelminthes group (which are very like the ancestors of the "Annelida" also), and the ancestors of the Echinodermata and Hemichordata may possibly be traced back to a similar stock (or to forms closely related to them) as well.

The Hemichordata are regarded by many authorities as a group which has departed but little structurally from the ancestral condition of the forms leading up to the vertebrate type of animal. From a study of their larvæ, some investigators have concluded that the Hemichordata are related to the Echinodermata; but this brings us no nearer to the solution of the problem, since the Echinodermata occupy an isolated position, and their ultimate affinities are very obscure. Although the Echinoderm line of development may lead back more directly to the Cœlenterata, there is a possibility of their forebears being quite closely related to the members of the Rotifera-Platyhelminthes group which have departed but little from the condition characteristic of the ancestors of the "Annelida" and other invertebrate groups; and even if the Echinodermata are to be regarded as the descendants of Cœlenterata-like forebears, it must be remembered that the ancestors of the Rotifera-Platyhelminthes group were themselves very closely related to the Cœlenterata, and would probably have been classed as such, rather than as colonial Protozoa.

It is quite possible to regard the line of development of the Echinodermata as related to the other two lines of development in question, and as branching off near, or

even further down in the developmental scale, than the points of origin of the lines of descent of the Hemichordata and the worm-like forms. It is also possible to suppose that in the hemichordatan line there have been carried over certain developmental tendencies from their common ancestry, such as the preservation of a "tornaria" larva characteristic of the Echinodermata, while in other respects the Hemichordatan line of development has paralleled that of the worm-like forms more closely, having taken over more of the tendencies which were to find opportunities for fuller expression in the worm-like forms from their ultimately common inheritance. Under these conditions the Hemichordata are related to both the Echinodermata and the worm-like forms, but their line of development has accompanied that of the worm-like forms much more closely and for a longer distance before each branched off along its own path of specialization. If the lines of development of the Hemichordata and of the worm-like forms have an ultimately common ancestry, and if both lines of descent have "travelled along the same developmental road" for a considerable distance before each branched off along its own path of specialization, it is not surprising that we find many structural resemblances in the two lines of descent, and the resemblance of such Hemichordata as *Cephalodiscus, Rhabdopleura, Phoronis,* etc., to certain "Polyzoa," may be as much the result of consanguinity as of "convergent development." This view enables us to harmonize the apparently discordant theories concerning the ultimate origin of the Vertebrata—all of which may contain a portion of the truth, as is frequently the case in the different hypotheses put forward to explain certain observed phenomena. Thus, according to this conception, we may derive the Vertebrata from forms similar to the Hemichordata, and still account for the annelid-like (and arachnid-like) features which appear in certain of the lower representatives of the vertebrate group, since tendencies present in the ancestors which ultimately

gave rise to both the Annelida and the Hemichordata are quite likely to appear in both Annelida and Hemichordata (or in forms descended from them, such as the Arachnida and the Vertebrata).[2]

One of the chief difficulties in the way of reaching a proper understanding of the mutual interrelationships of the different lines of development is the attempt to arrange these lines in the form of a dichotomously branching tree drawn in one plane—which is almost as impossible as the attempt to arrange all animals in a single linear developmental series; for it must be borne in mind that these different lines of development frequently approach one another from different directions, so that it would be necessary to represent their relationships by a figure drawn in *three* dimensions, rather than in a single plane. If this is done, it becomes easier to understand that the line of development of the "Annelida," for example, is paralleled (on different sides) by those of several other groups, and that all of these lines of descent may lead back to a common ancestry, or that their points of origin may be near the point at which the line of descent of the "Annelida" arose.

In discussing the ultimate relationships of the Vertebrata, Echinodermata, Mollusca, etc., the lack of intermediate forms annectent between the different developmental series, or connecting them with the supposedly ancestral forms, has made the subject of their affinities extremely speculative; and it is not until we come to the consideration of arthropod phylogeny that the evidence is at all satisfactory, and even here important gaps in the developmental chain leave much to be desired.

As was previously stated, the members of the Myzostomida-Onychophora group have developed many characters strongly suggestive of arthropod affinities; but they

[2] This statement should not be interpreted as implying that recent vertebrates are descended from living Hemichordata, etc., but it is merely intended to indicate that the Hemichordata have departed but little from the probable ancestral condition of the Vertebrata, and the same holds true for similar statements throughout this paper.

have become too greatly modified along their own lines of specialization in regard to those particular structures most frequently used in comparative morphology to be of much value for a phylogenetic study of the development of the different parts of the body in the lower arthropods. Among the "Annelida," on the other hand, we find some very promising material for such a study, especially among the chætopodan annelids, such as the Syllidæ (*e. g., Dujardinia rotifera,* etc.), which have segmented appendages, while others of the group have developed structures no less interesting from the standpoint of phylogeny, indicating that they have departed but little from the ancestral condition of the arthropods. The segmentation of the body of these annelids,[3] the nature and relative positions of the heart and the digestive, nervous and other systems, very readily lend themselves to such an interpretation, and it is not a difficult matter to derive the head region of a primitive arthropod from that of the annelid type (Bernard, 1892), or to derive the appendages of such an arthropod from those of the annelidan type, as has been recently discussed by Borradale, 1917.

In connection with the discussion of the derivation of the appendages of the lower arthropods from structures comparable to the parapodia of the annelids, it may be remarked that the attempt of Lankester, 1872, to derive the Arthropoda more directly from the Rotifera, such as the remarkable *Pedalion mira* (whose appendages and the "arms" of the male *Asplanchna* he compares to the movable spines of *Triarthra* and *Polyarthra*), has not been productive of as important results as those obtained from the comparison of the annelidan structures with those of the arthropods. This, however, is merely to be expected, since the annelids have developed far

[3] Just as some annelids are many-segmented, while the bodies of others are composed of fewer segments, it is quite reasonable to suppose that the ancestors of the arthropods exhibited a considerable range in the number of segments composing their bodies—and even among the most primitive arthropods there is a wide range in the number of segments composing their bodies.

more features in common with the lower arthropods than have such primitive forms as the Rotifera. On the other hand, the Annelida themselves (and hence ultimately the Arthropoda also) are the descendants of Rotifera-like (and Platyhelminthes-like) forebears, and it is quite possible that certain rotifers might develop features which later find opportunity for fuller expression in the forms descended from them (*e. g.*, the striated muscles of *Pedalion*); but, since the general organization of a rotifer's body is not so similar to that of the lower arthropods as is the case in the annelids in question, for the present at least it seems preferable to regard the slight resemblances between the appendages of the Rotifera and the lower Arthropoda mentioned above as the result of "convergence" (parallelism) in development rather than to consider it as a precocious development of structures later to be developed in the arthropod descendants of ancestors ultimately arising from rotiferan forebears. I would not utterly deny the latter possibility, however, since it may be quite possible that arthropods are to be derived more directly from Rotifera-like forebears (*e. g.*, *Hexarthra polyptera*, etc.) through forms related to the Tardigrada and *Nauplius*-like ancestors; but the great mass of evidence from comparative anatomy, embryology, etc., points to an "annelid ancestry" for the Arthropoda, and until other hitherto undiscovered forms have been found to indicate some other derivation for the group, we are safe in assuming that the "Annelida" represent as nearly as any known forms the ancestral condition of the Arthropoda.

In taking up the consideration of the evolution of the Arthropoda themselves, the question naturally arises as to what arthropods have departed the least from the probable ancestral condition of the group as a whole. Some investigators would claim that since the *Nauplius* larva is of such widespread occurrence among the lower arthropods, that it represents an ancestral type; but it must be borne in mind that a free-swimming larva is

usually very greatly modified in adaptation to its own mode of life and environmental conditions, and frequently represents an interpolated stage having no great phylogenetic significance (in comparison with the developmental stages of the embryo). Furthermore, it is extremely probable that the ancestral arthropods were not of one single type at all, but doubtless differed very greatly among themselves in size, the number of segments composing their bodies, etc., just as is the case among certain annelidan groups, or as is the case among the assemblage of lower arthropods comprising the most primitive members of the group next to be discussed.

The assemblage of lower arthropods comprising the Copepoda, Branchiopoda and their immediate relatives may be referred to as the Copepoda-Branchiopoda group. Its members include some of the most primitive of the arthropods, and it may be regarded as representing as nearly as any the forms giving rise to the different arthropodan lines of development. The Ostracoda represent a line of development which branched off at an early date, and should also be included in the group; but they are not structurally so important as the Branchiopoda, etc., for a phylogenetic study of the lines of descent to which the ancestral arthropoda gave rise. The Cirrepedia likewise represent a group which branched off from this stem at an early date, but they are too degenerate, and have followed their own line of specialization too far to be included among the primitive representatives of the Copepoda-Branchiopoda group. The Trilobita are very closely related to the Apodiæ and Branchiopoda in general, for such trilobites as *Nathorstia transitans* are somewhat annectent between the trilobites and the branchiopod *Opabina regalis* described by Walcott, 1912, and such trilobites as *Marella splendens* are very like certain Apodidæ, etc.; but the closest affinities of the Trilobita appear to be with the group next to be considered, and although the trilobites have preserved many very primitive features which might entitle them to a

position in the ancestral "Copepoda-Branchiopoda" group, it is preferable to consider them as members of the Trilobita-Merostomata group, with which they have much more in common.

The Trilobita-Merostomata group is composed of the Trilobita, Eurypterida, and Xiphosura, with their immediate relatives, and includes the forms which have departed the least from the ancestral condition of the arachnoids in general. The Trilobita are extremely closely related to the Merostomata, some of which (such for example as the fossil merostome *Bunodes lunula,* which has been admirably restored by Patten, 1912, or the cambrian merostomes, *Sidneyia inexpectans, Emeraldella brocki,* etc., described by Walcott, 1911–1912) bear well-developed antennæ very similar to those of the trilobites; so that the division of the Arthropoda into "Teleiocerata" and "Chelicerata" by Heymons, 1901, or into "Antennata" and "Chelicerota" by Boerner, 1909, can not be strictly applied when we take these forms into consideration. Walcott, 1912, considers that such merostomes as *Molaria spinifera* are connected with the trilobites through such intermediate forms as *Nathorstia transitans*—a trilobite also related to the Branchiopoda. Walcott also considers that the merostome *Sidneyia* represents a transition form between the trilobites and the eurypterids, and that the merostomes *Beltina* and *Sidneyia* are related to the ancestors of living Xiphosura; so that according to his views the trilobites are descended from branchiopods, while the eurypterids are descended from trilobites through such merostomes as his "Aglaspina" and "Limulava," from which living Xiphosura are descended.

In discussing the lower arachnoid forms, it is necessary to take into consideration the Pantopoda, which have apparently retained certain features strongly suggestive of crustacean affinities, while certain other features suggest that they are related to the arachnoid forms. Boerner, 1902, however, thinks that the Panto-

poda are structurally quite far removed from the arachnids examined by him, and since he has made a very extensive study of the different arachnoid forms, his opinion should have considerable weight. Since their line of development does not approach very closely to those of the other forms here discussed, the study of the Pantopoda is not of as great phylogenetic importance as that of those forms which occupy a position annectent between the other groups, or whose lines of descent approach those of the other groups. For the purpose of the present paper, it is therefore sufficient to say that the Pantopoda represent a highly aberrant group whose line of descent branched off at an early date, somewhere near the Trilobita-Merostomata group, and that they have followed a widely divergent path of specialization.

The scorpions are descended from forms very like the eurypterid members of the Trilobita-Merostomata group, and such eurypterids as *Glyptoscorpius* occupy a position annectent between the two groups. On the other hand, the scorpions, together with the Pedipalpi, are in many respects very like the ancestors of the higher arachnids, so that they form an ancestral group, the Scorpionida-Pedipalpi, intermediate between the Trilobita-Merostomata group and the higher arachnids. In the Scorpionida-Pedipalpi group should be included the closely allied pseudoscorpions and probably the *Koenenia*-like forms and the Solifugæ also.

Of the higher groups of arachnids, the spiders (Araneæ) are apparently quite closely related to the amblypigid (tarantulid) branch of the Pedipalpi, while the Phalangidea (Opiliones) and *Acarina* are more closely related to the pseudoscorpions and Solifugæ, although it has been suggested that the Cryptostemmatidæ occupy a position intermediate between the Pedipalpi (to which they are somewhat more closely allied) and the Phalangidea. The Linguatulida have been placed near the mites by many recent authorities on account of the supposed resemblance of their larvæ to such short-bodied mites

as *Phytoptus,* etc., and the apparent resemblance of the adults to eriophyid mites, so that provisionally, at least, the Linguatulida may be regarded as strongly aberrant mites, while the Tardigrada are probably not related to them, but to the Myzostomida, as has been previously discussed.

Since the arachnoid path of evolution has led off in a direction widely divergent from the path followed in the development of the Insecta, it is very difficult to understand how Thorell came to the conclusion that such highly developed arachnids (*i. e.,* those occupying a position far along the divergent line of development) as the Solifugæ are intimately related to insects. Furthermore, since the trilobite trend of development leads off toward the merostomes and the divergent evolutionary path of the arachnoid forms, it is necessary to search further back than the trilobites for a group standing more nearly in the direct line of development eventually resulting in the evolution of the insectan type, and for this purpose the study of the branchiopod representatives of the Copepoda-Branchiopoda group is much more valuable.

The members of the Copepoda-Branchiopoda group which seem to be the nearest to the stem forms at the base of the line of descent which ultimately leads up to the insect type of development are the Notostraca (Apodidæ) and anostracan Branchiopoda, which are likewise very closely related to the trilobites, so that certain ancestral features are to be found in the trilobites also, having been inherited from their common forebears; but, as was stated above, the trend of trilobite development is toward the production of the eurypterid and arachnoid type of development, and therefore leads away from the line of development which eventually results in the production of the insect type. Walcott, 1912, agrees with Bernard, 1892, in regarding the Apodidæ as among the lowest representatives of the Arthropoda (although certain copepods are also extremely primitive) and suggests

that the fossil annelids, *Canadia spinosa* (in which the head is bent down "so that the mouth faces posteriorly" in the position assumed by Bernard, 1892, to be that of the annelids which gradually took on the character of head region leading up to the arthropod type), and the Crustacea "were derived from the same general type of animal." The Copepoda represent a line of development which branched off near that of the Branchiopoda, at the base of the arthropod stem; and the Argulidæ (which are grouped with the Copepoda by Calman, 1909) are regarded by some authorities as annectent between the Copepoda and the Branchiopoda. The Ostracoda are related to both the conchostracan and cladoceran Branchiopoda (following Calman's classification) and the ancestors of the ostracods doubtless arose from forms intermediate between the Cladocera and Conchostraca. The Cirrepedia are apparently descended from ancestors related to both the Ostracoda and Copepoda, and their line of development branched off at an early date to follow their own strongly aberrant part of development.

Such anostracan branchiopods as the fossil *Opabina regalis*, whose structure according to Walcott, 1912, "is very suggestive of an annelidan ancestor," and such notostracan branchiopods as the fossil *Burgessia bella* (which has sessile eyes and hepatic glands in a carapace resembling that of *Lepidurus*) serve to indicate what the first arthropods were probably like, and they occupy a position near the base of the stem-forms whose lines of development were eventually to produce the insectan type of arthropod. The fossil notostracan branchiopod *Waptia* occupies a position annectent between the above-mentioned branchiopods and the malacostracan group next to be considered.

The leptostracan (phyllocarid) group occupies a position intermediate between the rest of the Malacostraca and the branchiopods described above. They have also carried over from their common branchiopod ancestry certain features likewise inherited by the trilobites; but.

as was previously stated, the trilobites do not stand in the direct line of descent of the Leptostraca, and those characters which they possess in common were inherited from their common branchiopod ancestry, and can not be interpreted as indicating that the trilobites represent the ancestral forms giving rise to the lepostracan type. The fossil leptostracan *Hymenocaris* is evidently related to the fossil branchiopod *Waptia* (which occupies a position intermediate between the branchiopods and Leptotraca), but *Hymenocaris* is clearly a leptostracan, and resembles such living forms as *Nebalia,* while the fossil leptostracans *Carnavonia* and *Tuzoia* resemble such living Leptostraca as *Nebaliopsis typica* in the character of the carapace, etc. The closer affinities of the fossil Ceratiocaridæ, etc., have not been determined, due to the imperfect preservation of the limbs, etc., but they clearly belong to the leptostracan group. There is much to be said in favor of including the Leptostraca in the next group of the Malacostraca to be considered, but from the standpoint of a phylogenetic study it is preferable to consider the Leptostraca (together with other primitive forms not yet described) as nearer the ancestral forms from which the other Malacostraca were derived.

A further stage of development is represented by the Anomostraca-Cumacea group which includes the Syncarida and a portion of the Peracarida of Calman's classification, together with their immediate relatives. The Anomostraca (Anaspidacea and Bathynellacea of Chappius, 1915), Mysidacea and Cumacea are very closely interrelated, and all of them exhibit affinities with the Leptostraca, so that the members of the leptostracan group might well be included here also; but they have been treated as a separate group, to emphasize the fact that they occupy a position annectent between the Branchiopoda and the Malacostraca (with which their strongest affinities lie). Although the members of Anomostraca-Cumacea group are extremely closely related to the Tanaidacea, the closest affinities of the Tanaidacea

are with the Isopoda (and Amphipoda), so that it is preferable to consider them with the latter group. The Anomostraca-Cumacea group is of the greatest phylogenetic importance, since its members have departed as little as any known forms from the probable ancestral condition of the higher Crustacea, Insecta and "Myriopoda" (*sensu lato*).

The Mysidacea have retained some primitive characters indicating their connection with the Leptostraca-like forms which preceded them, and they are quite like the ancestors of the eucaridan (euphausiacean and decapodan) members of the higher crustacean groups. They are also probably related more remotely to the ancestors of the aberrant hoplocaridan (stomatopodan) line of development, and through such forms as the Cumacea they are connected with the ancestors of the Tanaidacea (and therefore of the Isopoda also). They are not so important for a phylogenetic study of the insects, etc., however, as the Anomostraca and Cumacea (with the Tanaidacea) are. The Cumacea occupy a position intermediate between the Mysidacea and the Tanaidacea, being somewhat more closely allied to the latter. They are also related to the Anomostraca (Syncarida), as is true of the Mysidacea, the interrelations of the different members of the group being rather complicated.

From the standpoint of the study of the phylogeny of the insects and their relatives the Anomostraca and Cumacea (together with the Tanaidacea) are by far the most important forms, since the ancestors of the insects and their relatives were doubtless descended from forms closely related to the Anomostraca, Cumacea, and Tanaidacea. Of these three, the Anomostraca are apparently the most ancient (fossil remains of the others have not yet been found), and have doubtless departed as little as any from the ancestral forms which were eventually to give rise to the isopods, insects and "myriopods." The fossil Pleurocaridæ (*e. g., Acanthotelson,* etc.) are nearer to the living genera *Koonunga, Anaspides, Para-*

naspides, etc., while the fossil "Gampsonychidæ" (*e. g.,* "*Gampsonyx,*" *Palæocaris* and *Gasocaris*) are nearer the living genus *Bathynella.* Such fossil forms as *Præanaspides* found in the Carboniferous rocks is extremely like the living *Anaspides* which has apparently preserved many ancestral characters, but little modified, to the present time. The Anomostraca are related to the Leptostraca, but no forms intermediate between them and the Leptostraca have yet been described, and it is possible that the line of descent of the Anomostraca leads back to the branchiopods through Leptostraca-like forms not yet discovered. Superficially, at least, such slender branchiopods as *Yohoia tenuis,* etc., resemble certain members of the Anomostraca, and it is possible that the slenderer, more cylindrical Anomostraca, such as *Bathynella,* may have inherited the tendency toward the slender form of body from anostracan branchiopods of the *Yohoia* type. In *Bathynella* the eyes have become completely lost, but in *Koonunga* sessile eyes are found and their presence suggests that sessile-eyed forms may have developed from the *Koonunga* type. In *Anaspides* the eyes are stalked.

From ancestors occupying a position intermediate between the Anomostraca and Cumacea (and also related to the Mysidacea) have arisen the lines of descent leading to the isopod Crustacea, Insecta, and "Myriopoda" (s. l.). The Tanaidacea (Chelifera) which occupy a position near the base of the isopod stem are very closely related to the Anomostraca, Cumacea and Mysidacea, and, together with the Isopoda and Amphipoda (which are descended from ancestors very similar to them), they might be included in the Anomostraca-Cumacea group; but if the Isopoda-Amphipoda group is considered separately, the Tanaidacea must be included in the latter group, since their closest affinities are with the Isopoda. The Amphipoda are quite closely related to the Isopoda, and their ancestors may also have arisen from forms intermediate between the Anomostraca and Cumacea

(and also related to the Mysidacea), so that the sessile-eyed character occurring in the group might be regarded as a retention of the tendency toward the formation of sessile eyes exhibited by such primitive forms as *Koonunga,* while the slender body form present in such Amphipoda as the caprellids, *Rhabdosoma,* etc., may possibly be due to the retention of the tendency toward the slender form of body (such as that present in the more primitive *Bathynella*) in forms which are otherwise rather highly modified. The Isopoda-Amphipoda group originated very close to the point of origin of the insect line of development, and the two lines have paralleled one another extremely closely. Since the members of the Isopoda-Amphipoda group have not travelled so far along the path of specialization in following the same developmental road with the insects, they have retained many primitive features characteristic of the ancestors of the insects (and "myriopods"), and such forms as *Apseudes* are particularly interesting for a phylogenetic study of insects and their immediate relatives.

The Symphyla-Pauropoda group (composed of such forms as *Scolopendrella, Scutigerella, Pauropus, Eurypauropus,* and their immediate relatives) contains the forms which appear to be very near the base of the "myriopod" stem, and which have retained a great number of features characteristic of the ancestors of insects, so that a study of the structures of the Isopoda-Amphipoda group and the Symphyla-Pauropoda group are of the greatest importance for a proper conception of the nature of the first insects to be evolved. The Symphyla-Pauropoda group probably also arose from forms occupying a position intermediate between the Anomostraca and Cumacea, and likewise closely related to the Tanaidacea which originated from similar forebears. Such Anomostraca as *Bathynella* have not departed far from the ancestral condition of the Symphyla-Pauropoda group, and although they have developed many modifications along their own line of specialization, they are as

near as any known forms to the ancestors of the Symphyla, etc. The Symphyla-Pauropoda group in turn has departed but slightly from the ancestral condition of the "Myriopoda" as a whole, although the ancestral "Myriopoda" comprised forms with bodies composed of more numerous segments as well as those made up of fewer segments. From ancestors similar to the members of the Symphyla-Pauropoda group one line of development has led to the chilopod type of myriopod, while the other has led to the diplopod type. From their ancestors related to the members of the Symphyla-Pauropoda group, the Chilopoda have carried over many characters also inherited by the ancestors of insects, so that a structural study of the Chilopoda is of considerable value from the standpoint of insect phylogeny (as is true to a lesser degree of the Diplopoda also).

As was stated above, the ancestors of the Insecta were related to the members of both the Isopoda-Amphipoda group (including the Tanaidacea) and the Symphyla-Pauropoda group, so that the lines of descent of all three groups (insects, isopods and Symphyla) doubtless had a common origin in forms intermediate between the Cumacea and Anomostraca (and also related to the Mysidacea), and all of the three groups have inherited from their common ancestry many characters also carried over in the lines of development of the other two of the three groups in question. The common ancestors of the three groups just mentioned (insects, isopods and Symphyla) were not of any one single type, but doubtless differed quite markedly among themselves in the number of segments composing their bodies, the slender or stouter and flatter character of the body and other features. Some of them were more like the Tanaidacea, while others were more like *Bathynella* and other members of the Anomostraca, etc., and this should be clearly borne in mind in attempting to determine what the ancestors of the insects, etc., were like; for the greatest obstacle to arriving at the realization of the true nature

of the ancestors of insects and their relatives has been the attempt to derive them all from one type of creature —which is manifestly impossible, since even the lowest representatives of any group differ markedly among themselves, and their ancestors also must have differed markedly among themselves (although not to such a great extent as their progeny do).

Although such Anomostraca as *Bathynella* have become specialized along their own lines of development, they have retained many features which suggest what some of the ancestors of the insects and Symphyla must have been like, and I think it very probable that the ancestors of *Scolopendrella* and the Protura were quite similar in many respects to *Bathynella,* while other apterygotan insects, such as *Machilis,* have carried over more characters from the tanaidacean side of their common ancestry. Therefore, if we accept the idea that some of the common ancestors of insects, isopods and Symphyla occupied a position intermediate between the lines of development of the Anomostraca and the Cumacea-Tanaidacea, and differed a little less among themselves than the Anomostraca do from the Cumacea-Tanaidacea, it becomes perfectly clear that some apterygotan insects could inherit from the tanaidacean side of their common ancestry characters which also appear in the isopods which are derived from Tanaidacea-like forebears; while on the other hand, other apterygotan insects could inherit from the *Bathynella* side of their common ancestry certain characters which also appear in the Symphyla or other forms descended from *Bathynella*-like forebears.

The Protura (such as *Acerentomon, Eosentomon,* etc.) are the most primitive representatives of the Insecta, and have inherited from their common ancestry many features also preserved in the "Myriopoda"; and the embryological development of the apterygotan group to which they belong has much in common with that of the "Myriopoda," as has been pointed out by Philiptschenko,

1912, Lignau, 1911, Chamberlain, 1917, Heymons, and others. The retention of the stumps of three pairs of legs on the abdominal region (in addition to the three pairs of thoracic legs) at first caused some zoologists to doubt that the Protura are really insects (since the idea that such forms with vestigial abdominal legs could not be true "hexapods" if they had more than six limbs seemed to stand in the way of their realizing the true insectan nature of the Protura), but the overwhelming evidence of their structural organization has convinced all recent entomologists that the Protura are true insects. As pointed out in a recent paper (Crampton, 1916) the Protura are quite closely related to such other Apterygota as *Tomocerus;* and, with the Entomobryids and Sminthurids, they constitute the non-styli-bearing division of the Apterygota.

Of the styli-bearing Apterygota, the next group to be considered, which may be referred to as the Campodeoid group, comprises the Rhabdura (*e. g., Campodea*), the Dicellura (*e. g., Projapyx, Japyx,* etc.) and their immediate relatives. Dicellura, such as *Projapyx, Anajapyx,* etc., have segmented cerci, and occupy a position intermediate between the Rhabdura, such as *Campodea,* and the other Dicellura, although their closest affinities are clearly with the Dicellura. The Campodeoid group, whose members have entognathous mouth parts and vestigial abdominal legs suggestive of the proturan structures, occupy a position intermediate between the lower apterygotan Protura and the higher apterygotan forms, such as *Nicoletia, Lepisma,* etc., which also belong to the styli-bearing apterygotan subdivision which includes the Campodeoid group as well (Crampton, 1916). The Campodeoid group, while inheriting certain features from the symphylan side of their common ancestry, have inherited in addition certain other features more typical of the crustacean side—which likewise reappear in the isopod-amphipod descendants of their common ancestors.

The Lepismoid group, composed of the lepismids,

machilids, and their immediate relatives, is quite closely connected with the Campodeoid group in the styli-bearing subdivision of the Apterygota; but their mouth parts are ectognathous, and in their general organization they approach remarkably closely to the lower Pterygota; so that they may be said to occupy a position annectent between the lower Pterygota and the Campodeoid group. The members of the Lepismoid group seem to have inherited more characters from the crustacean side of their common ancestry than from the symphylan side, while the members of the Proturan group seem to have inherited more characters from the symphylan side, and the members of the Campodeoid group appear to partake to some extent of characters occurring in both the crustacean (isopod) and symphylan sides of their common ancestry.

It might be possible to explain the presence of both crustacean (isopod) and symphylan characters in the insectan stem by supposing that the crustacean, insectan and symphylan "currents" in the "onward flow of life," although acquiring more and more of a distinct individuality as their "waters" emerge from the common stream at their source, nevertheless have an intermingling or commingling of contiguous waters as they flow side by side, before ultimately diverging too greatly for such an intermingling. This idea, however, might in a sense be interpreted as meaning that the Symphyla-like insects were descended from Symphyla, and the Crustacea-like insects from Crustacea (*i. e.*, isopod Crustacea), whereas insects as a whole were probably not "polyphyletic," but all insects were derived from a common ancestral source. The forms composing this common ancestral source, however, differed among themselves very greatly, although the amount of divergence was probably not too great to prevent their being grouped in a single class—or possibly even in a single subclass or order. In this ancestral-insectan group, there were doubtless isopod-like insects which resembled the most

insect-like representatives of the ancestral isopods, while the Symphyla-like members of the ancestral-insectan group must have resembled the most insect-like representatives of the ancestral Symphyla. In other words, at the common level at which the lines of descent of the isopods, insects and Symphyla originated, some of the ancestral insects (which differed greatly among themselves) occupying the "hereditary territory" contiguous to that of the ancestral Symphyla would inherit certain developmental tendencies in common with or similar to those also inherited by certain Symphyla; and similarly, some of the ancestral insects occupying the "hereditary territory" contiguous to that of the ancestral isopods would inherit certain developmental tendencies similar to those of certain isopods and the same principle would apply to successively larger, as well as to the smaller groups in any evolutionary study. According to this view, certain developmental or "inherent" tendencies exhibited by the isopods or myriopods might also appear in insects if the opportunity of manifesting themselves should arise, and this would merely imply that these tendencies were inherited from an ultimately common ancestry, rather than that some insects were descended from isopods while other insects were descended from Symphyla, etc. Some evolutionists might object to the use of such terms as "inherent tendencies" on the ground that they savor too strongly of "vitalism"; but, so far as I can see, the expression "inherent tendencies" means much the same thing as a part of "heredity," and one implies no more of a predilection toward vitalism than the other does.

Although their closest affinities are with the Campodeoid group and the Apterygota in general, certain members of the Lepismoid group are structurally remarkably similar in many respects to such primitive Pterygota as the stone-flies and may-flies, so that Handlirsch, 1906, who has completely disregarded the close interrelationships of the Apterygota, and their evident ancestral character (with reference to the winged insects) in his

attempt to derive the Pterygota more directly from trilobites, is forced to assume that the lepismids may represent degenerate Pterygota! Their whole sturctural organization clearly proclaims in no uncertain terms that the closest affinities of the lepismids are with the rest of the Apterygota, with which they are connected by intermediate forms, and a careful study of the comparative anatomy and embryology of the Apterygota, "Myriopoda" and Crustacea can result in no other conclusion than that the Apterygota have departed as little as any known forms from the condition characteristic of the ancestors of the Pterygota. The lepismids are therefore no more to be considered as degenerate Pterygota, than apes are to be considered as degenerate men—unless one reverses the whole scheme of evolution; and under such conditions there would be nothing to prevent any one from assuming that trilobites are degenerate lepismids, or any other equally improbable reversing of the evolutionary sequences!

In connection with the supposedly "degenerate" condition of the Apterygota, I would take issue with the implication carried in such statements as that by Tothill, 1916 (p. 376), who would claim that the Apterygota "are highly specialized animals as indicated by the frequent reduction of mouth parts, visual organs, tracheæ, etc.; and by the development of peculiar structures such as the caudal spring and collophore." In the first place, it is inadmissible to judge the ancestral character of any group by the condition of its most highly specialized members, as Tothill appears to do in the case of the Apterygota, since any arthropodan group, no matter how low it may be in the scale of development (*e. g.*, Copepoda, etc.) may include certain members which have become very highly specialized along their own lines of development without affecting the general position of the group as a whole; and in a phylogenetic study we must consider the most primitive representatives of the group, rather than the most highly specialized ones, if such a study is to yield any tangible results. If Tothill had

therefore considered such lowly organized Apterygota as *Eosentomon*, *Anajapyx*, etc., instead of the highly specialized *Anurida*, *Sminthurus*, etc., I am sure that his opinion of the "degenerate" condition of the Apterygota as compared with the Pterygota would have been quite the opposite of that expressed in his paper. Furthermore, there are practically no arthropods known which are primitive in all respects, and, as is the case throughout the whole realm of zoology, forms which have retained many features in an exceedingly primitive condition may be very highly specialized in other respects; so that one must take into consideration the composite primitive features of the group as a whole; and, just as the most primitive members of the Pterygota are studied in an attempt to determine their ancestry, so the most primitive members of the Apterygota must be considered in such a phylogenetic study.

Even in the matter of the nature of their eyes, such forms as *Machilis* (which are related to *Lepisma*) can hardly be called "degenerate," and in the face of the fact that in the trilobites themselves there occur at least three types of eyes—"isolated eyes or ocelli, aggregate eyes of biconvex lenses, and compound eyes" (Tothill, p. 321, quoted from Lindstrom, 1901), it is very improbable that the type of eyes found in *Lepisma* are of a higher type than the compound eyes of the Pterygota. As far as their mouth parts are concerned, I find the lepismids much more primitive than the Pterygota (with the possible exception of nymphal ephemerids) and Boerner, 1908–1909, has called attention to crustacean structures so similar to those found in the maxillæ, etc., of apterygotan insects, that there can be no doubt that the mouth parts of the Apterygota in general instead of being "degenerate" have retained many more primitive features than those of most lower Pterygota.

As far as the number of abdominal segments is concerned, some Apterygota, instead of having fewer segments, have even retained twelve, and in these forms, such as the Protura, there is also a postembryonic in-

crease in the number of segments (from nine to twelve in the abdomen) comparable to the increase of segments in the "Myriopoda," so that Tothill's statement that "in the Hexapoda numerous investigations have shown the segments arise only during the egg stage" does not hold in the case of the Protura. There is also one other point in Tothill's paper which might easily lead to error unless properly explained: namely, that his discussion of the nature of the appendages of the abdomen in a "larval" *Stenodictya* is based upon a figure taken from Handlirsch's book, the supposition being that it represents the restoration of an actual fossil larva, whereas in reality the figure is purely a figment of Handlirsch's imagination, for no known insects have biramous abdominal legs, and even the supposedly biramous condition of such specialized structures as the maxillæ of insects is now thought to be a secondarily acquired feature, and not a retention of an originally biramous condition (Borradale, 1917). Tothill's suggestion of a derivation of winged insects directly from Chilopoda (which represent a side branch from the symphyloid main stem of myriopod development) without reference to the apterygotan forms is open to all of the objections raised against deriving winged insects from apterygotan forms without having any of the advantages of the latter hypothesis, and if the latter is untenable, the idea of deriving winged insects from chilopods is infinitely more so!

Despite the fact that trilobites are on a divergent branch leading away from the main line of insectan development (*i. e.,* leading off to the arachnoid development) Handlirsch, 1906, would derive winged insects directly from trilobites, wholly ignoring the Apterygota, Symphyla, Tanaidacea, and all of the other anatomically intermediate forms—which would be exactly on a par with an attempt to derive the "Nordic" race of men directly from lemurs (or rather from *cats,* whose line of development has deviated from the main line of evolution leading to the development of the human type) wholly ignoring the Mongolians, Australoids, Neanderthaloids,

Heidelberg man, *Pithecanthropus*, the great apes, and all other anatomically intermediate types! His line of argument is somewhat as follows: winged insects occurred at an extremely early period, and no fossil Apterygota dating back to so ancient a period has yet been discovered; therefore Apterygota are more probably a recent degenerate offshoot, rather than forms standing more nearly in the line of development of winged insects—a line of reasoning which caused the earlier Coleopterologists to reverse the evolutionary sequence and attempt to derive true beetles from the snout beetles, until further discoveries brought to light the fact that true beetles were geologically as ancient, or more ancient, than the snout-beetle type, which comparative anatomy clearly showed must have been derived from, and therefore could not be ancestral to, the true beetles! As experience has shown, the paleontological evidence, which at best is of a most fragmentary and incomplete nature, must supplement that of comparative anatomy (of adults or embryos)—and even in the case of the paleontological evidence it depends wholly upon comparative anatomy here also; and furthermore many fossils were themselves as highly specialized along their own lines of development as the most primitive living forms are (some of which have retained just as many ancestral characters and are as little modified in certain respects as those forms which fell by the wayside at an early date). Paucity in numbers of individuals among the Apterygota, their usually small size and fragile nature, have all contributed to make their fossil remains extremely rare, and under these conditions the lack of remains from earlier strata can not offset the weighty argument of comparative anatomy and embryology in favor of regarding them as the nearest representatives of the type ancestral to winged insects.

As for deriving winged insects directly from trilobites on the ground of the faint resemblance of trilobites to insects in regard to their possession of a certain type of eye structure, antennæ, and lateral projections of the tergal region (woefully inadequate resemblances in com-

parison with the multitude of resemblances between insects and their real ancestral forms), it may be said that these same structures are likewise shared by such fossil merostomes as *Bunodes lunula* and on precisely the same grounds, insects should be derived from merostomes also (a manifest impossibility) since these have the same ancestral qualifications of great antiquity, and they possess the trilobite type of antennæ, eyes and lateral tergal projections! When one studies the embryological development of insects, however, it is evident that their ancestors had *two* pairs of antennæ instead of the one pair apparent in trilobites, and the insectan type of head is nothing like that of a trilobite in which the head region is not set off by a marked constriction with well-defined mandibles, maxillæ and underlip of the insectan type, while the head region and mouth parts of isopod and amphipod Crustacea, etc. (with their two pair of antennæ, insectan type of head, mandibles, maxillæ and underlip), are clearly similar in character to what the ancestors of insects must have been like, and the same holds true of the legs and terminal appendages, etc., in these Crustacea. Therefore, as far as comparative anatomy is concerned the Crustacea, with their progeny the Symphyla, etc., are, beyond any possibility of doubt, the nearest forms to the ancestors of insects in general, and this is also borne out by embryology, which, however, can not be applied in the case of the trilobites; so that here we must depend largely upon comparative anatomy, whose verdict is unmistakably in favor of the Crustacea, Symphyla and Apterygota as the ancestral forms leading up to the pterygotan type, and is unmistakably against considering the trilobites anywhere near the immediate ancestors of winged insects or even in their direct line of descent. On this account, it is most astonishing that nearly all recent writers (Schuchert, 1915, Ruedemann, 1916, Lull, 1917, etc.) have accepted without reservation such startlingly revolutionary ideas as those proposed by Handlirsch—and upon such meagerly insufficient grounds when one looks into the subject at

all! Such implicit faith in this age of skepticism speaks volumes for the weight of Handlirsch's authority among paleontologists, but the true morphologist prefers the direct evidence of his own observation to any "*petitio ad auctoritatem*" especially when such startlingly revolutionary ideas as those which Handlirsch proposes are based upon no firmer foundation than a vague resemblance which will not even bear the test of close scrutiny.

When one turns to the published figures of the earliest fossil insects for some light upon the nature of their body structures, his eye is met by a dreary succession of disembodied wings, and in the rare instances in which the body parts are also figured, only the vague outlines are given with a nonchalant disregard for the vital details so necessary for any phylogenetic study; and one can not help wondering what impression the "pterophilous" paleontologists would have of their subject if the tables had been reversed and they had been presented with merely the vaguest outlines of a series of wings containing no veins or other important structures, in the expectation that such figures would be of any value for a phylogenetic study! Furthermore, many living "synthetic" types are quite devoid of wings (as it true of immature forms also) and the study of these forms is in some cases even more important than that of the wing-bearing ones (*e. g.*, *Timema*, *Grylloblatta*, nymphal Plecoptera, *Lepisma*, etc.), but how are we to compare them with a series of disembodied wings? So far as one can judge from the figures of fossil insects, we have living to-day certain lowly organized forms which are in many respects just as primitive as these fossil forms (which are also specialized to some extent) and when the paleontologist returns again and again to a comparison with living forms for an interpretation of fossil structures, the suspicion becomes a conviction that a study of the primitive characters of various lowly organized living insects is just as instructive from a phylogenetic point of view, and is infinitely more satisfactory than a laborious reconstruction of fossil fragments.

The different theories concerning the origin of the wings of pterygotan insects were discussed in a recent paper (Crampton, 1916) in which it was pointed out that it is possible to consider that the wings of insects were derived from paranotal outgrowths of the tergal region of apterygotan forms, Crustacea, etc., which are ultimately homologous with the paranotal outgrowths of the trilobites, without attempting to derive the wings from these trilobitan structures without the intermediation of other ancestral forms. Not only do the lepismids exhibit paranotal structures (lateral tergal outgrowths) which are homologous with the precursors of wings, but the lepismoid forms (*Lepisma, Nicoletia, Machilis,* etc.) approach remarkably closely to the pterygotan type in many respects, and may be considered as annectent between the remainder of the Apterygota and the lower Pterygota.

The lowest representatives of the Pterygota, or winged insects, constitute the Perlid-Ephemerid group, composed of the Plecoptera, Ephemerida, and their immediate relatives. The modern representatives of the group are in many respects fully as primitive as certain of their fossil relatives, although it is necessary to turn to some such extinct forms as the "Protephemeroidea" and Palæodictyoptera to find the connecting forms annectent between the Plecoptera and the ephemerids. The immature Plecoptera are remarkably similar to lepismids in the nature of the head outline, mouth parts, thoracic sclerites, etc. (Crampton, 1917*a*), and even in regard to their terminal abdominal structures the lepismids are very like Plecoptera (Crampton, 1918*a*), but the Plecoptera have lost the median terminal filament, which, however, is still retained in the ephemerid members of the group. The ephemerids, and the Odonata, represent somewhat aberrant types of development which branched off at an early date to follow their own paths of specialization, although they have not proceeded very far along this road. The Plecoptera, on the other hand, have carried over in their line of inheritance a great many characters which were to become further developed in the higher groups of in-

sects, and they appear to have departed as little as any from the ancestral condition of these groups, so that they are as important as any synthetic types, with the possible exception of the Palæodictyoptera, for a phylogenetic of winged insects in general. The great antiquity of fossil Plecoptera is also in harmony with the idea that the Plecoptera are quite like the ancestors of the higher forms, and since the anatomical and phylogenetic data are in complete harmony in this respect, we are justified in assuming that the Plecoptera have departed as little as any forms from the ancestral condition of the groups next to be considered.

The Plecoptera, embiids, and Dermaptera originated from essentially similar ancestors, which were not far removed from present-day Plecoptera, and their lines of descent have followed a common developmental road for a considerable distance, before first the embiids, and a little later the Dermaptera branched off to follow their own paths of specialization (Crampton, 1917*a*). The *Hemimerus*-like forms branched off from the Dermapteron stock at an early date, and a little later, the Coleopteron type was differentiated. The Strepsiptera were possibly differentiated from a similar stock still later. The terms "earlier" or "later" as used above are employed in the sense of indicating the relatively lower or higher level along a line of development, at which a group branched off, and is based upon the comparative anatomical primitiveness of the group under consideration. In the case of the Coleoptera, Handlirsch maintains that they are paleontologically older than the Dermaptera, and if subsequent findings should corroborate this view, it would be necessary to search for the origin of the Coleopteron line of development lower down on the Plecopteron stem than the point at which the Dermaptera branched off to follow their own path of specialization, but the Dermaptera are so much more lowly organized than the Coleoptera, to which they are anatomically very similar (see also Crampton, 1918*b*), that I am inclined to believe that the lack of earlier Dermapteron remains is due to the incom-

pleteness of the fossil record, rather than to the absence of Dermapteron forms antedating the Coleoptera.

The Isoptera, blattids and mantids seem to have originated from a stock similar to the members of the Plecopteron group mentioned above (Crampton, 1917*a*) and they apparently branched off at a very early date to follow their own developmental road for a short distance before each of the three separated to follow its own path of development. The Isoptera are anatomically intermediate between the members of the Plecopteron group, and the rest of the blattid group (with which the Isoptera seem to have somewhat stronger affinities than with the members of the Plecopteron group, although they are related to the embiids and Dermaptera quite closely). This might be taken to indicate that the Isoptera are more primitive than the blattids, as is borne out by certain of their anatomical features; but on the whole, the blattids seem to be somewhat more lowly organized and, according to Handlirsch, the Isoptera are paleontologically much younger than the blattids. It is quite probable that the Zoraptera described by Silvestri, 1913, are an offshoot of the isopteron stock.

The orthopteroid insects, grylloblattids and phasmids were descended from ancestors very similar to *Grylloblatta* recently described by Walker, 1914, and such phasmids as *Timema* are also very near the base of the orthopteroid stem. These insects have inherited many characters from the plecopteroid side of their ancestry, and they also share many features in common with the blattoid group mentioned above (see Crampton, 1917*a*). Their line of descent is apparently ultimately traceable to a plecopteroid ancestry (as is probably also the case with the blattoid forms), but their line of development branched off very near that of the blattoid group, and they continued to parallel the path of development of the latter group for a considerable distance before diverging along their own branch of specialization. The grylloblattids seem to be somewhat closer to the ancestors of the gryllids and "locustids," while the phasmids may be

nearer to the ancestors of the "acridids," although the line of development of the latter may have branched off from a "locustid" stock. The *Phyllium*-like forms seem to be modified phasmids which have certain features in common with the grasshopper group.

The plecopteroid, blattoid and orthopteroid groups are all very primitive, and are so intimately connected by intermediate forms or synthetic types that they are to be considered as representing one section of the Pterygota, to which the term "Plecopteradelphia" was applied (Crampton, 1916*a*) to indicate that they are the immediate descendants of Plecoptera-like ancestors and the ephemerids and Odonata should doubtless be included in the same section of the Pterygota. There is a bare possibility that the blattoid forms rather than the Plecoptera are nearer the ancestral type from which the others were derived, but the close resemblance of immature Plecoptera to lepismids, and the very primitive organization of the Plecoptera, make it very probable that they, rather than the blattids, represent very closely the ancestral forms which gave rise to the blattids themselves, and the other types mentioned above. The higher insects were also apparently descended from forms ultimately derived from ancestors related to the Plecoptera, but they have "clustered together" in another division forming the "Neuropteradelphia" (Crampton, 1916*a*) or forms grouped about the Neuroptera in the second section of winged insects next to be considered.

The members of the second section (or "Neuropteradelphia") fall into two principal groups. One of these, comprising the psocids, Thysanoptera, and hemipteroid forms, were probably descended from ancestors not unlike the psocids, and it is also quite possible that the Mallophaga, and the Anopleura or "Siphunculata," represent offshoots of this stock. This group had a common origin with the neuropteroid insects (probably from Plecoptera-like forebears) and the two paths of development have extended side by side for a considerable distance, both having numerous characters in common.

The Neuropteron group comprises the Neuroptera, Trichoptera, and Mecoptera, with their immediate relatives. They and their descendants are very closely related to the members of the psocid group mentioned above, and the two lines soon merge in a common ancestry when traced back toward the plecopteroid stem. The Neuroptera seem to be a very ancient type, and have inherited certain primitive characters which would indicate that their line of development branched off at a comparatively low level. Both the Trichoptera and the Mecoptera are descended from ancestors quite like the present-day Neuroptera, while the Lepidoptera branched off near the trichopteron line of descent, and the Diptera branched off near the mecopteron line (see also Crampton, 1917*b*). The Siphonaptera were apparently descended from ancestors not unlike phorid Diptera.

The Hymenoptera represent a somewhat aberrant group having affinities with both the members of the psocid and neuropteron groups. Their line of descent probably originated near the point at which the psocids and Neuroptera branched off, and they inherited many features also present in the members of both of these groups, so that their line of development must have accompanied or extended beside those of the other two for a considerable distance before it branched off to follow its own path of specialization.

Summary

The points which should be especially emphasized in regard to the evolution of the insectan branch of the arthropod lines of development may be briefly summarized as follows:

The ancestors of arthropods were not of any one type, but varied in regard to the number of segments composing their bodies, the outline of the body, etc.; and while some of them may have been as small as the tardigrades, it is more probable that the types would be included between the extremes represented by the Onychophora and

the Annelida, or even between the extremes included within the annelidan group itself.

The first arthropods also were not of one single type, but possibly varied as greatly among themselves as a branchiopod-like copepod would differ from a copepod-like branchiopod, etc. It is very probable that the stem forms eventually giving rise to the line of development leading up to the production of the insectan type of arthropod would be included in the branchiopod group.

The next stage in the evolution of the insectan type of arthropod is represented by forms related to the leptostracan group, although the Leptostraca do not include all of the types representing this stage of development. It is possible that the Trilobita may be considered as somewhat near these forms, since they exhibit a few characters in common with them, but the trilobitan line of descent is not directly in line with the insectan path of development, since it diverges toward the evolution of the merostomes and eurypterids leading off toward the arachnoid type of development and away from the insectan type.

A further stage of development is represented by the members of the group including the Anomostraca, Cumacea and Tanaidacea. While they doubtless also resembled the other members of this group in certain respects, it is quite possible that the ancestors of insects and "myriopods" varied between the extremes represented by *Bathynella* among the Anomostraca and by such forms as *Apseudes,* etc., among the Tanaidacea, from which the Isopoda, etc., were also descended. *Bathynella,* with no eyes, with its cylindrical body, reduced legs and "stumpy" pair of pleopods, basal limb appendages suggesting the precursors of styli, short terminal appendages, etc., must be very like the ancestors of the Protura and Scolopenrelloid forms; while such Tanaidacea as *Apseudes,* with its flagelliform terminal uropods, and the type of head appendages, etc., present in the Isopoda in general suggest the type of ances-

tors giving rise to those Apterygota which are provided with flagelliform terminal appendages.

The members of the Symphyla-Pauropoda group have retained many characters present in the ancestors of the "Myriopoda" and Insecta. The Chilopoda are an offshoot from this stock and do not stand quite as near the direct line of development of the insectan type.

The Apterygota are the nearest known representatives of the ancestors of winged insects, and while the first insects to be evolved possibly were of types resembling both the proturan forms and the campodeoid forms (or even the machiloid forms), the lepismid type approaches as nearly as any known forms to the lowest representatives of the Pterygota.

The first winged insects resembled the lepismids in many respects, and their nearest living representatives are the ephemerids and Plecoptera. The Plecoptera and the fossil Palæodictyoptera stand at the base of the lines of descent of the higher forms, and, since the line of descent of the Plecoptera has accompanied those of the higher forms for a longer distance, they are even more important than the Palæodictyoptera for a phylogenetic study of the evolution of higher insects. Most higher forms cluster about the Plecoptera and Neuroptera as nuclei representing synthetic types of the greatest importance, and both types are of considerable antiquity, although the Neuroptera were possibly ultimately descended from forms not unlike the Plecoptera (and ephemerids).

It is quite improbable that insects or arthropods in general (as well as the more inclusive groups) are of a polyphyletic origin. The ancestors of insects, for example, were of several types, some resembling the ancestors of isopods, while others resembled the ancestors of the Symphyla, etc., and the lines of development of all three extend for some distance side by side before each begins to diverge from the others. Those insects resembling Symphyla were not descended from symphylid forebears nor were those insects which resemble isopods descended

from isopod forebears, but the symphylid and isopod characters which appear in certain insects were inherited from their ultimately common ancestry, and the relative positions of the different ancestors of insects in the "hereditary areas" of this common ancestry (*i. e.*, whether their hereditary areas were contiguous to those of the ancestors of isopods or to the ancestors of the Symphyla, etc.) determines whether certain of the insects descended from them shall resemble isopods or Symphyla, etc., and the same principle applies in the successively larger as well as in the smaller groups of living things.

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